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Mines and galls on fossil leaves from the Late Cretaceous of southern Negev, Israel

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ABSTRACT

The recently described Late Cretaceous (Turonian) flora of Israel contains 46 species of angiosperms. Traces of galling and mining activity are exceptionally abundant and well-preserved. In a collection of more than 1000 specimens of terrestrial and aquatic angiosperms, almost all the leaves were affected. The mines consist of several morphological types, showing varying degrees of specialisation with respect to leaf histology. Some are readily identified with modern mine types; others may represent extinct types. Characters potentially useful for morphological classification of fossil mines are discussed and illustrated. Exuvial remains attributable to cecidomyiian dipterans suggest pupation in the gall, an advanced feature of this group. These findings are evidence of rapid evolution of mining and galling habits during the rise of early angiosperm-dominated communities.

KEY WORDS: Angiosperm evolution, galls, mines, palaeominology, plant-insect co-evolution, Cretaceous, Israel.

INTRODUCTION

For a long time, preservation of mine and gall traces on fossil leaves was considered an exceptionally rare phenomenon, a palaeontological curiosity. Hering (1951: 300) wrote that, although such traces deserve attention, “we cannot, however, expect from this source any new evidence on the origin of the mining habit”. Owing to recent advances in the field (Labandeira *et al*. 1994; Labandeira 2002*a*, *b*) we can now speak of palaeominology and palaeocecidology, fruitful branches of palaeontological research. Fossil mines and galls provide direct evidence of the evolution of parasitic behaviour, and of plant responses to such parasitism. So preserved mines and galls are thus potentially significant since they may contribute towards a better understanding of co-evolution.

For this potential to be realised, fossil mines and galls must be studied on a regular basis. This requires a morphological classification, based on distinctive trace morphologies, such as “morphonomes” for mines and “cecidimorphs” for galls, as operational units. A few mine traces from the Late Cretaceous and Cainozoic have been named after modern genera that produce similar mines (Frič 1882; Kernbach 1967; Kozlov 1988). Morphological classification was introduced for a few Neogene galls (discussed in Brooks 1955; Strauss 1977; Waggoner & Poteet 1996).

This paper deals with certain features of fossil mines, including mine configuration with respect to leaf histology, frass deposition, consumption pattern of leaf tissue, and the succession of consecutive mine instars. These are features on which an ichnotaxonomic system of categorisation can be based. I also discuss examples of distinctive gall morphology.

The recently described Late Cretaceous (Turonian) flora of Israel (Krassilov *et al*. 2005) contains 46 species of angiosperms. The remains of terrestrial and aquatic plants occur in the Upper Shale Member of the Ora Formation, bracketed between carbonate

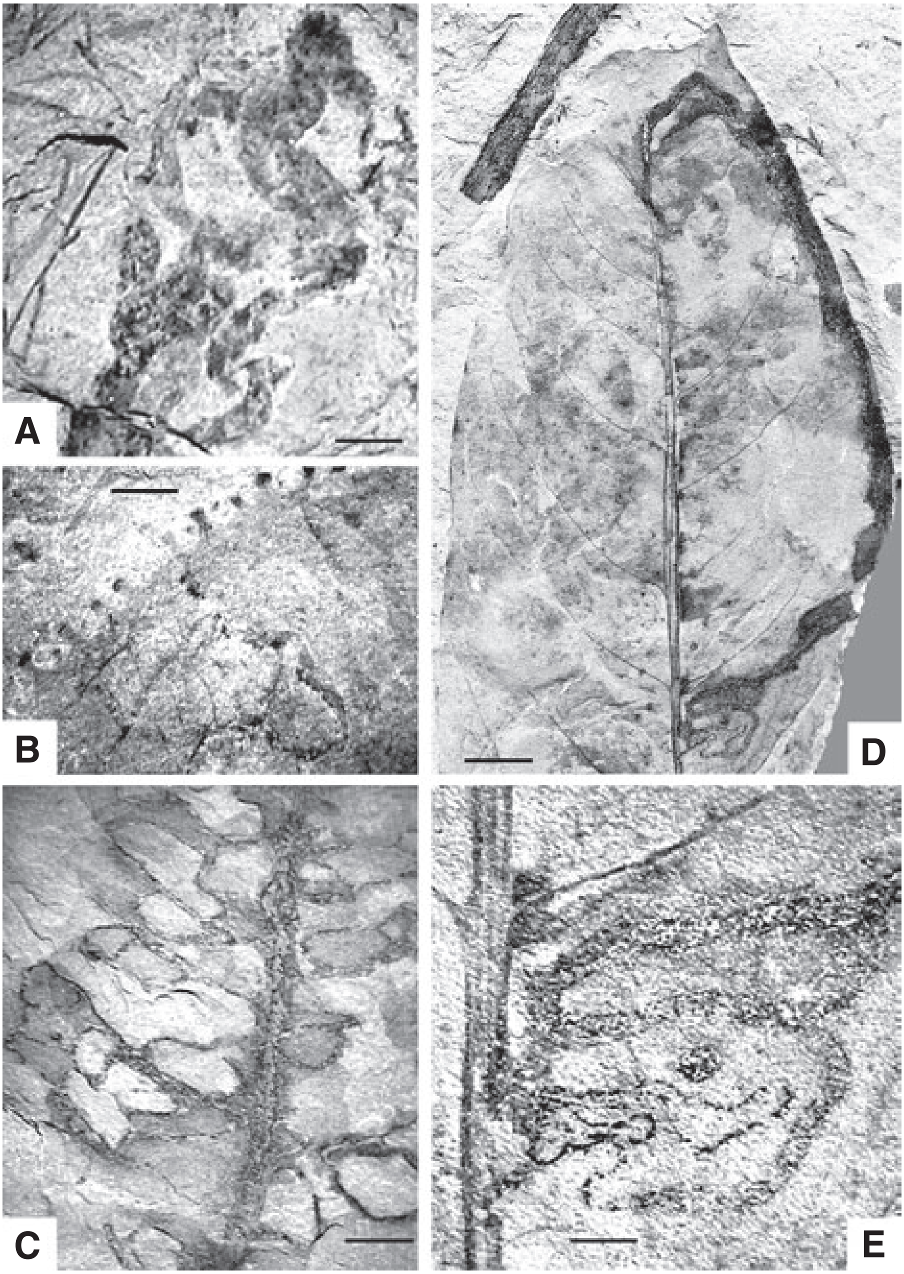

Fig. 1. Mines of Lepidoptera on Cretaceous (Turonian) leaves from the southern Negev: (A) intestiniform mine (visceronome) on *Platydebeya papilionacea*, IG1-1; (B) leaf-margin mine on *P. papilionacea* looping before the exit through a marginal gland, IG1-45; (C) two generations of blotch mines on *Dewalquea gerofitica,* IG1-644; (D) an ophiostigmatonome on *P. papilionacea*, departing between the lateral veins, arching along the margin and approaching the midrib for construction of the terminal chamber, IG1-139; (E) end-blotch of the same mine with a hibernation cocoon, frass deposited as small grains in the gallery but as slender threads in the end-blotch. Scale bars: (A) 1 mm, (B) 1.4 mm, (C) 2.7 mm, (D) 5 mm, (E) 1 mm.

sequences with mid-Turonian ammonites. The orders Ranunculales, Nymphaeales, Nelumbonales, Trochodendrales, Hamamelidales, Juglandales, Rosales, Myrtales, and Sapindales are recognised, with varying degrees of confidence, among the dicotyledons; the Najadales, Pontederiales, Arales, Cyclanthales, Arecales, and Typhales, among the monocotyledons. Modern aspects of the Turonian angiosperms from the southern Negev suggest a high rate of morphological macroevolution accompanied by ecological differentiation. Taphonomic observations have revealed that several plant assemblages are present, viz. mangroves, marshes, back-mangrove freshwater macrophytes and inland broadleaved woodland. The earliest angiosperm mangroves are inferred on the basis of taphonomic evidence, root morphology and cryptoviviparous propagules. Some flower/fruit remains indicate combretaceous and rhizophoraceous affinities of the Cretaceous mangrove species.

MATERIAL AND METHODS

Traces of mining and galling activity are exceptionally abundant and well preserved. In the collection of more than 1000 specimens of terrestrial and aquatic angiosperms, almost all the leaves are affected. The material is preserved as subcrustations or mineral films deposited beneath the cuticle, especially for epidermal mines, which are therefore even more conspicuous than in fresh leaves.

The traces were observed and photographed with a LEICA MZ6 stereomicroscope and LEICA DFC320 digital camera. The terminology for mine configuration is after Hering (1951), and for galls after Meyer (1987). The collections are deposited in the Institute of Evolution, University of Haifa, Israel, depository collection IG1.

RESULTS

Leaf Mines

About 20 distinct mine morphotypes are recognised, some of which are illustrated in Figs 1–4. The most frequently parasitised leaves are those of what is believed to be the mangrove species with supposed affinities to the Myrtales: *Paltydebeya papilionacea* Krassilov, *Eudebeya angusta* Krassilov, and *Dewalquea gerofitica* (Dobruskina) Krassilov. Leaves of extant mangroves are mined by lepidopteran caterpillars and, to a lesser extent, by Coleoptera and Hemiptera (Farnsworth & Ellison 1991). Moth attacks may even cause defoliation of mangroves (Witten & Damanik 1986), and the abundance of fossil leaves bearing lepidopteran traces may suggest similar events in the Cretaceous. *Paltydebeya papilionacea* is more vigorously attacked by miners than other species, with about 10% of leaf area lost. As in present-day mangroves (Hogarth 1999), the differences might have been due to the relative toughness of the leaf blades and their nitrogen content (C:N ratio, Feller 1995).

Fig. 1D shows a linear-blotch mine coiled at the ends (an ophiostigmatonome) starting at the midrib, running to the margin and extending parallel to it. This trajectory allowed the larva to avoid the stronger proximal parts of the lateral veins that thinned and curved distally before the margin. Several small blotches were formed along the way marking developmental shifts of the consecutive instars. The terminal portion of this mine turned back toward the midrib, a secure place to pupate, and a terminal chamber with a cocoon was formed. Frass was deposited as small pellets in the channel, but arranged in slender

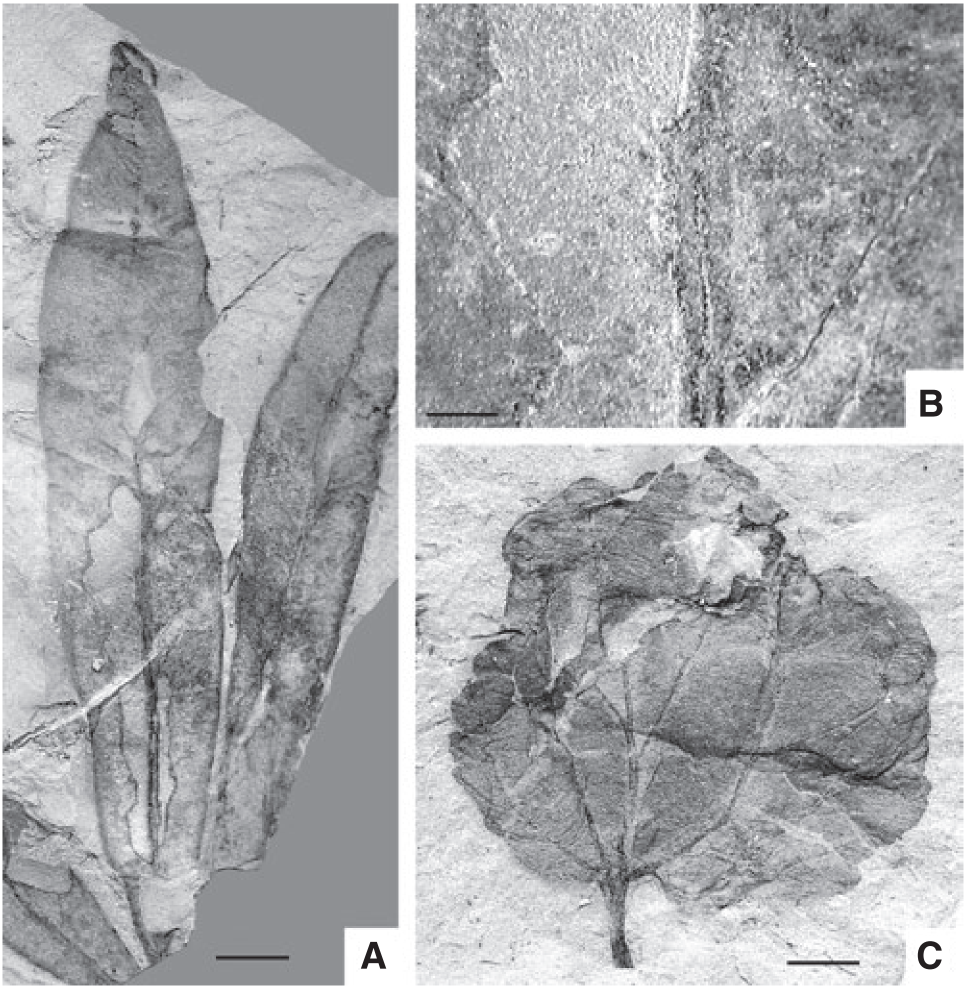

Fig. 2. (A, B) window feeding on *Dewalquea gerofitica,* IG1-847; (C) deformed leaf of *Eocercidiphyllites glandulosus* mined over the basal veins, IG1-747. Scale bars: (A) 0.3 mm, (B) 1.2 mm, (C) 0.4 mm.

threads toward the terminal chamber, reflecting a dietary change related to development of the mouthparts. The behavioural pattern of mine construction is the same as in many present-day Lepidoptera, which can be taken as evidence of a fully developed mining behaviour in mid-Cretaceous species.

Some types of blotch mines (stigmatonomes) and intestinally coiled mines (visceronomes: Figs 1A, 1B) find their analogues in the mines of the lepidopteran taxa *Lithocolletis* (Lyonettidae) or *Stiamella* (Nepticulidae) (Braun 1917). Marginal mines in the material are most common on the leaves with marginal glands, a source of sugar-rich sap. However, the terminal segments of such mines have deviated from the leaf margin, forming a meandering loop across the lateral veins, ending in an exit through the gland (Fig. 1B).

Examples of "epidermal windows", with all the tissues removed except the two epidermal layers (Figs 2A, 2B), suggest a feeding habit typical of coleophorid miners that spend only part of their larval life in the mine. Indeed, mines coursing along leaf margins may end in an elongate or semicircular incision, and cases built of cut-out leaf pieces are attached at or near the incision site. These leaf pieces are loosely coiled as in present-day coleophorid cases. The attachment of the cases is almost parallel to or at 45° to the leaf margin (Figs 3C–E), depending on whether the orientation of the mouth opening occurs at right angles or obliquely to the long axis of the case. Both mouth types occur in some extant lepidopteran species of *Coleophora* (Coleophoridae) (Hering 1951).

Heavily mined leaves sometimes show two generations of overlapping mines: one of relatively small elliptical dark blotches, the other of larger irregular lighter ones with meandering margins (Fig. 1C). Such differences commonly occur between successive larval instars of miners, the early one (forming small dark blotches) feeding on leaf tissues, mostly epidermis, of a higher nutritional quality than the later one, which thereby excavates larger areas and removes most of the tissue. The change of habit may suggest a seasonal hardening of leaf tissue making it less palatable. Such changes will be most pronounced during brief, dry periods which may occur between consecutive instars of miners.

A peculiar type of linear trail with two parallel-sided rows of large well-spaced frass pellets is characteristic of some dipteran (Agromyzidae?) mines. Adjacent tracks in opposite directions (retractonomes) may form very large blotches, occupying almost half of the leaf blade, but never crossing the midrib (Figs 4C, 4D)*. In other cases, tracks diverge in all directions, forming an asteronome (Figs 4A, 4B). The first type was produced by a species that oviposited approximately midway between the midrib and leaf margin, whereas the second type indicates an oviposition site on the midrib.

For leaves with palmate venation, mine trails sometimes diverge from the point of the petiole insertion and extend along primary veins. Such leaves are more or less deformed, often inequilateral and notched at the apex (Fig. 2C).

Among the aquatic plants, both aerial and floating leaves of *Nelumbites* (Nelumbonaceae, Nelumbonales) are mined, the latter showing a peculiar type of elliptical stigmatonome coarsely spun over the margins, with occasional loose stitches extending inside the loop (Figs 5A–C). No closely comparable structures have been found in any of the insect groups having mouthpart spinnerets. Lepidoptera (*Lithocolletis*) sometimes bind frass grains by spinning at the periphery of the mine, but their mining of floating leaves is unusual, whereas chironomid miners of Nymphaeaceae and Potamogetonaceae (Berg 1950) typically construct linear mines.

Galls

Galls are often found on the same leaves as mines. For example, *Dewalquea gerofitica* is infested with conical acuminate galls about 3 mm long, rather evenly spaced along the thickened margin and scattered between the lateral veins. These galls are sometimes so dense that the leaf blade is scarcely exposed at all (Figs 3A, 3B). The galls protrude

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* C. Labandeira in his review of this paper has suggested that the infected area may represent damselfly oviposition. However, the arrangement of traces does not correspond to a typical pattern of zygopteran egg sets and seem more compatible with a frass-pellet interpretation. Additional material is needed to support this hypothesis.

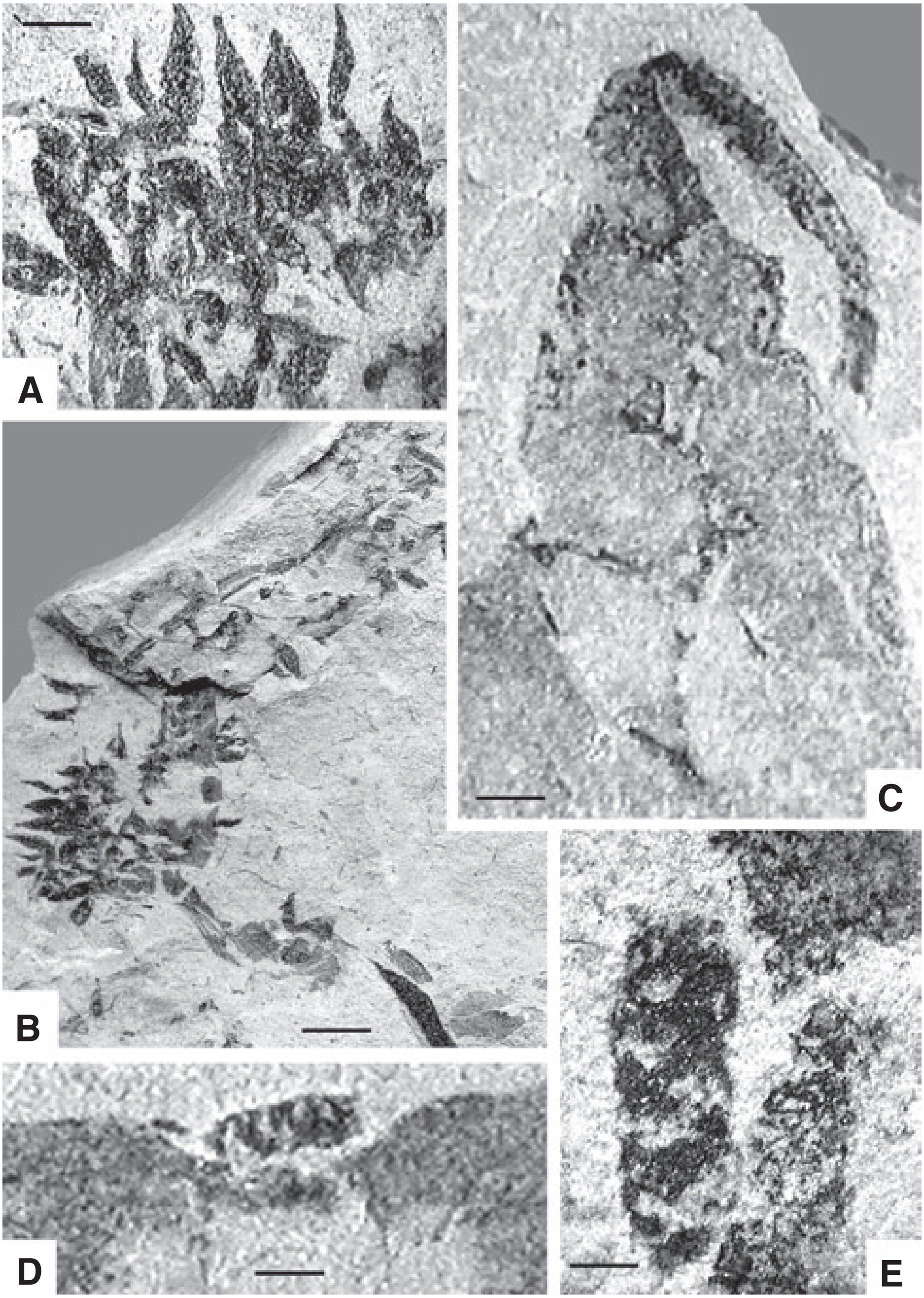

Fig. 3. Galls and larval cases on *Platydebeya papilionacea*: (A, B) leaf surface densely covered with conical galls, IG1-618; (C) tubular case attached at leaf tip almost parallel to marginal incision, IG1-191; (D, F) case of a coiled leaf piece cut out of leaf margin and attached at about 45° (classified as mouth type 3, see: Hering 1951), IG1-109. Scale bars: (A) 1.6 mm, (B) 5 mm, (C) 0.6 mm, (D) 1 mm, (E) 0.4 mm.

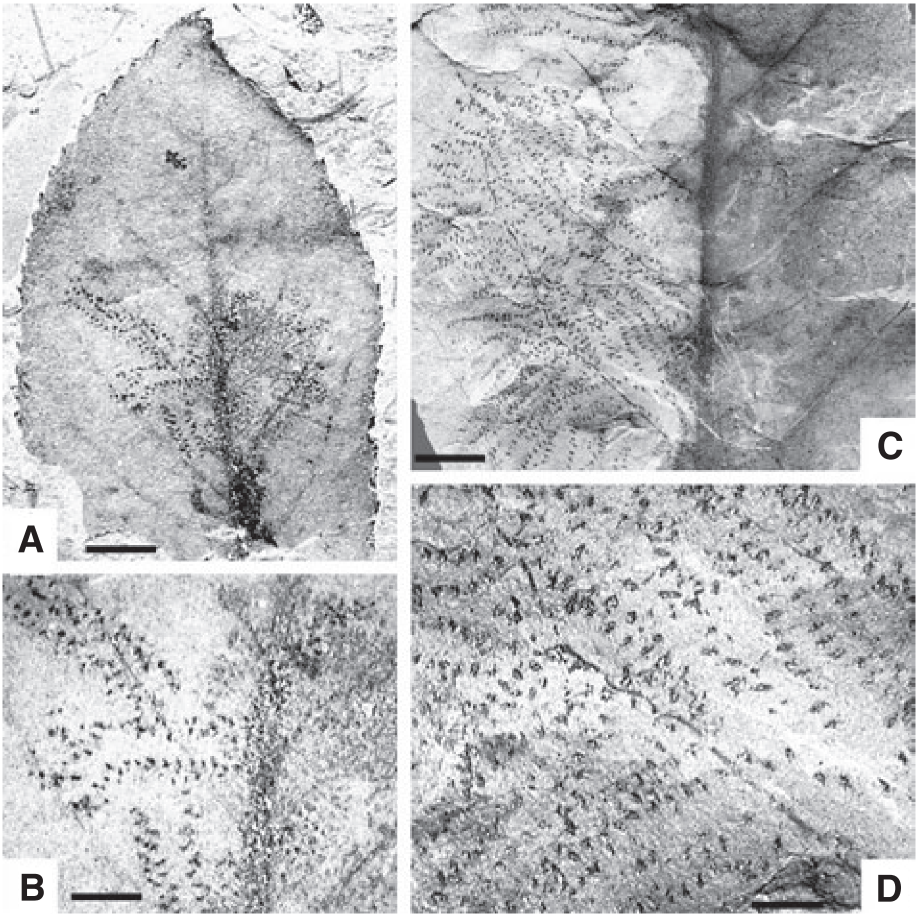

Fig. 4. Dipteran mines on *Platydebeya papilionacea*: (A, B) mine tracks with two rows of frass pellets diverging from the midrib, IG1-138; (C, D) half-blade covered with closely aligned track segments in opposite directions, with two rows of frass pellets, IG1-11. Scale bars: (A) 2.5 mm, (B) 1.2 mm, (C) 4 mm, (D) 1.3 mm.

from the upper leaf surface, opening on to the lower surface, with a disk of thickened epidermal tissue around a circular hole. An imprint of a larva preserved among the galls (arrow in Fig. 6A) shows the posterior end with five abdominal segments, while the anterior part is immersed in the growing gall.

Galls of the same type occur on *Platydebeya papilionacea*, possibly confirming its taxonomic affinities with *Dewalquea*. A detached gall (Fig. 6B) shows a neatly cut abscission area at which it was separated from the basal disk that remained on the lower side of the leaf, as in modern gall midges. Among fossil cecidia, similar structures are figured for cynipid galls on Miocene oak leaves assigned to the cecidimorph genus *Antronoides* Waggoner & Poteet, 1996 (Cynipidae, Hymenoptera) and compared to extant *Antron clavuloides* Beutenmuller (Waggoner & Poteet 1996). These galls differ from the Cretaceous cecidimorph mainly in the narrower fusiform shape and the apical bottleneck. However, the appendages emerging from the opening are here interpreted

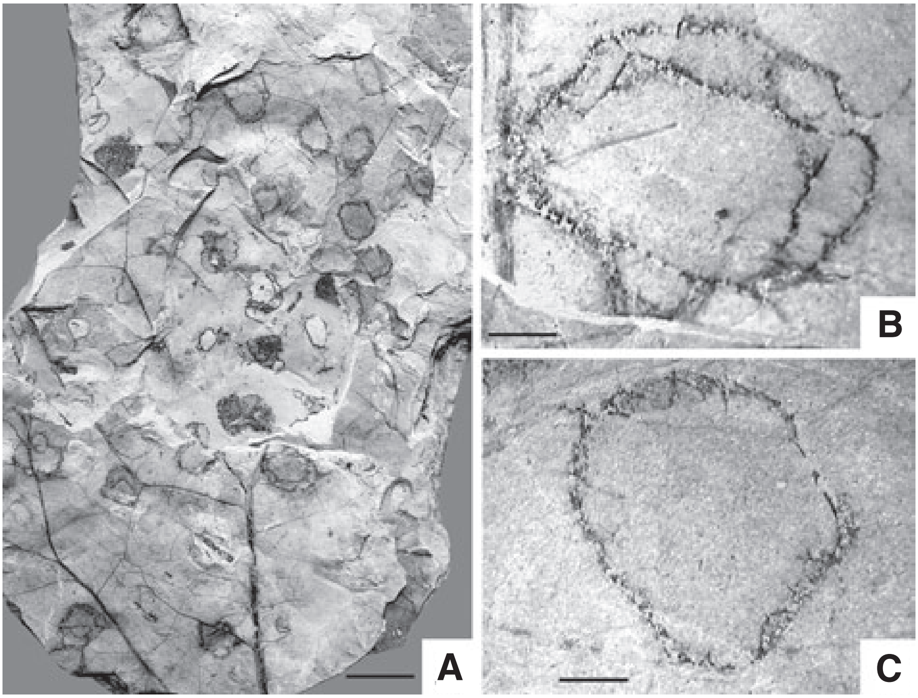

Fig. 5. Spun blotch mines on floating leaves of *Nelumbites aravensis*, IG1-11; note loose stitch in (B). Scale bars: (A) 10 mm, (B, C) 1.2 mm.

as exuvial remains of a gallicolous pupa. More specifically, antennal horns and cephalic setae are used by gall midges to cut their way out of the gall (Gagné 1994). Some fruits from the same locality resemble these types of organoid galls, suggesting a role of gall induction in angiosperm organogenesis.

DISCUSSION AND CONCLUSIONS

The feeding and habitation traces on Cretaceous angiosperm leaves from Gerofit, southern Negev, show evidence of insect groups, principally Lepidoptera and Diptera, that are not represented among the body fossils from the same locality, which consist mainly of Orthoptera and Coleoptera. The diversity of mine types in the Turonian of the Negev is much higher than in any leaf assemblage of the preceding geological ages (reviewed in Boucot 1990; Labandeira *et al*. 1994; Scott *et al*. 1994), including the Cenomanian assemblage of Lebanon (Krassilov & Bacchia 2000), which suggests explosive evolution of the mining habit. Diverse serpentine mines on platanoid leaves from the Turonian of Kazakhstan (Kozlov 1988) indicate a simultaneous increase in numbers of mining insects in other regions.

The mine types differ in the configuration of the mine track; their course with respect to the leaf margin, midrib and laterals, and frass deposition; and features related to the duration and significance of each mining stage in the life cycle. These features include the presence of a cocoon, window feeding, leaf cutting and construction of larval cases. Fly mines are readily distinguishable from moth mines, and occasional *Cladophora*-

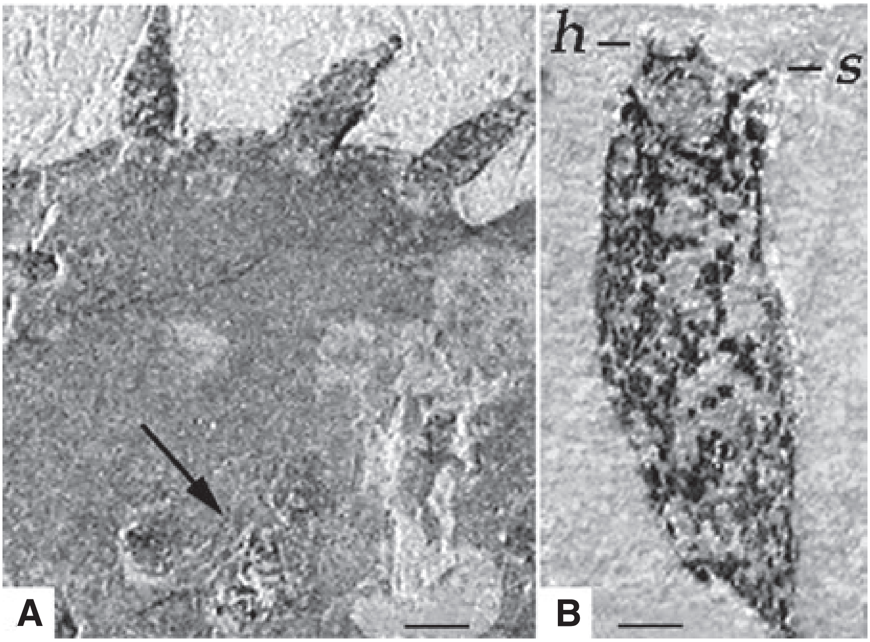

Fig. 6. Galls on Cretaceous leaves from the southern Negev: (A) fruit-like organoid galls on *Dewalquea gerofitica*, arrow on larva overgrown by developing gall, IG1-277; (B) abscised gall showing exuvial appendages (h, antennal horns; s, cephalic setae), IG1-110. Scale bars: (A) 1.2 mm, (B) 0.4 mm.

type mining (Hering 1951) is recognisable among the latter. Most of the mine types appear fairly modern, suggesting a fully developed mining habit. However, no extant analogues are found for certain types of mines on floating leaves, suggesting a possibility of extinct mining habits. Overlapping generations (Fig. 1C) indicate seasonality of mining activity, a potential source of climatological inference.

Although some leaf mines developing from the point of the petiole insertion caused deformities of the leaf blade (Fig. 2C), no intermediates between mining and galling were found. These two habits were as different in the Cretaceous as they are today. Galling habits were no less advanced than those of leaf mining, lending no support to the theory of their origin from one another (reviewed in Meyer 1987).

Galls are known since the Late Carboniferous (Van Amerom 1973; Labandeira & Phillips 2002), but advanced galling habits are commonly held to appear through gradual co-evolution of gall-inducing arthropods and angiosperms during the Tertiary (Ananthakrishnan 1984). Fossil evidence is inconsistent with this latter hypothesis. The mechanism of gall dehiscence by breaking loose from the leaf, as well as pupation in the gall rather than in the soil, are advanced developmental features (Mani 1964) that appeared in the mid-Cretaceous, at the critical stage of angiosperm–arthropod co-evolution. The role of galling as an organogenic factor in the evolution of early angiosperms is poorly understood, but some similarities of gall structure to the reproductive parts of the same host plant suggest that this role was significant.

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